NeoBiota 17: 1–18 (2013)
doi: 10.3897/neobiota.17.4841
www.pensoft.net/journals/neobiota

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Body size changes in passerine birds introduced to New Zealand from the UK

Tim M. Blackburn[1], Melanie J. Monroe[2], Becki Lawson[3], Phillip Cassey[4], John G. Ewen[3]

1 *Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK, and Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, South Africa* **2** *Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, 06520-8106, USA* **3** *Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK* **4** *School of Earth & Environmental Sciences, University of Adelaide, SA 5005 Australia*

Corresponding author: *Tim M. Blackburn* (tim.blackburn@ioz.ac.uk)

Academic editor: *Daniel Sol* | Received 8 February 2013 | Accepted 24 April 2013 | Published 28 June 2013

Citation: Blackburn TM, Monroe MJ, Lawson B, Cassey P, Ewen JG (2013) Body size changes in passerine birds introduced to New Zealand from the UK. NeoBiota 17: 1–18. doi: 10.3897/neobiota.17.4841

Abstract

One feature of global geographic variation in avian body sizes is that they are larger on isolated islands than on continental regions. Therefore, this study aims to assess whether there have been changes in body size following successful establishment for seven passerine bird species (blackbird *Turdus merula*, song thrush *T. philomelos*, house sparrow *Passer domesticus*, chaffinch *Fringilla coelebs*, greenfinch *Chloris chloris*, goldfinch *Carduelis carduelis,* yellowhammer *Emberiza citrinella*) introduced from the continental islands of the UK to the more isolated oceanic landmass of New Zealand in the middle of the nineteenth century. Measures of tarsus length were taken from individuals from contemporary UK and New Zealand populations of these species, and from historical specimens collected around the time that individuals were translocated from the UK to New Zealand. Analysis of Variance was used to test for size differences between contemporary UK and New Zealand populations, and between historical UK and contemporary UK and New Zealand populations. Historical UK populations have longer tarsi, on average, than 12 (7 UK and 5 New Zealand) of the 14 contemporary populations. Significant decreases in tarsus length relative to the historical populations have occurred in the UK for blackbird, chaffinch and greenfinch, and in the New Zealand blackbird population. Contemporary New Zealand house sparrows have significantly longer tarsi, on average, than both historical and contemporary UK populations. Exposure to novel environments may be expected to lead to changes in the morphology and other traits of exotic species, but changes have also occurred in the native range. In fact, contrary to expectations, the most common differences we found

were between contemporary and historical UK populations. Consideration of contemporary populations alone would underestimate the true scale of morphological change in these species over time, which may be due to phenotypic plasticity or genetic adaptation to environmental changes experienced by all populations in the last 150 years.

Keywords
Body size, Exotic species, Historical population, New Zealand, Passerine Bird, Tarsus length

Introduction

The traits possessed by species are not fixed, but change in response to a variety of selective forces. The rate of evolution is typically slow (Haldane 1949), meaning that significant trait change is not observed in most species in most human lifetimes. However, more rapid change is possible when species are exposed to new adaptive zones (Futuyma 1979), and so one set of species for which selective forces may change rapidly is those introduced by humans into areas well beyond the limits of their natural geographic distributions. The abiotic and biotic interactions such exotic species experience in their non-native ranges may differ substantially from those in their native ranges (Blackburn et al. 2009, Davis 2009). As a result, we might therefore expect to see relatively fast trait changes in exotic species, through either or both of the processes of genetic adaptation or phenotypic plasticity.

In the second half of the nineteenth century, European colonists introduced more than 100 exotic bird species to the isolated archipelago of New Zealand, as part of organized attempts to naturalise a range of useful and ornamental species there (Thomson 1922, Duncan et al. 2006). Many of these species originated in the European homelands of the colonists (Thomson 1922, Long 1981), and subsequently proceeded to establish viable populations in New Zealand, where they are now widespread and abundant components of the avifauna (Robertson et al. 2007). These species provide a golden opportunity to explore the factors influencing life history trait variation in wild populations, as a series of replicates in a natural experiment on the effects on these characteristics of translocation to a new environment on the opposite side of the planet.

Several studies provide evidence that reproductive life history traits differ between exotic New Zealand populations and native populations of the same bird species in their location of origin. For example, hatching failure rates tend to be higher in New Zealand than in native populations, in inverse proportion to the number of individuals introduced, suggesting an effect of the population bottleneck on this reproductive trait via increased levels of inbreeding (Briskie and Mackintosh 2004). Nine out of eleven species of passerine established in New Zealand following introduction from the UK have significantly smaller clutch sizes, and less seasonal variation in clutch size, in their exotic ranges (Evans et al. 2005; see also Samaš et al. 2013). Eight of these species also show reductions in clutch volume in New Zealand compared to the UK (Cassey et al. 2005). The results for clutch size and its seasonal variation are consistent with

Ashmole's hypothesis that variation is driven by the effect of seasonality on resource availability per adult bird (Ashmole 1963), as New Zealand is less seasonal than the UK (Evans et al. 2005), and also match patterns of variation shown by island native bird species relative to their mainland relatives (Covas 2011).

While there is evidence for changes in reproductive traits, to date no study has tested for differences in body size in the native and New Zealand exotic ranges of bird species. Yet, body size is a fundamental characteristic, which tends to correlate strongly with other aspects of a species' life history (Peters 1983). Moreover, there are good grounds to expect that body size will change following introduction to New Zealand.

First, one of the primary features of global geographic variation in avian body sizes is that they are on average larger on islands relative to continental regions, and larger at higher latitudes (Olson et al. 2009). The latitudinal relationship is best explained by variation in temperature and seasonality, through the effects of body size on thermal physiology and starvation tolerance in times of resource scarcity (Olson et al. 2009). Size differences between island and continental birds have been hypothesized to result from differences in thermal physiology (Clegg and Owens 2002, Olson et al. 2009), ecological release from competitors and predators, intensified intraspecific competition, and immigrant selection (Lomolino 2005), although the actual drivers are currently unknown. As New Zealand is one of the most isolated landmasses on Earth, one might expect size increases in species introduced there, especially from continental regions (while UK is also an archipelago, it is barely isolated from continental Europe, and most British bird populations exchange individuals with those on the continent). Conversely, New Zealand lies closer to the Equator than the UK (c. 35–45°S versus c. 50–60°N), and has a more temperate climate on average. If latitude or temperature is the primary driver of size variation, we might expect size decreases in species introduced to New Zealand. However, latitude and insularity might counteract each other and lead to no changes in body size.

Second, the largest members of bird genera are likely to be island taxa more often than expected by chance (Meiri et al. 2011), suggesting again that insularity is accompanied by increase in body size. In fact, recent natural colonists to New Zealand do tend to be smaller than their closest endemic relative, suggesting that isolation on New Zealand is accompanied by increase in body size (Cassey and Blackburn 2004). This effect is more prevalent in smaller birds (taxa <250g): larger-bodied colonists may be larger or smaller than their closest endemic relative with about equal likelihood. However, these size differences may not reflect natural selection within populations as much as different survival, establishment or immigration abilities of species. If so, we may not necessarily see size changes following introduction (but see the next paragraph).

Third, several case studies of recent natural or human-mediated avian colonizations of islands identify differences in body size associated with colonization. For example, Clegg et al. (2002) show that the natural sequential colonization by silvereyes (*Zosterops lateralis*) from Tasmania to South Island, New Zealand (in 1830), and the Chatham Islands (in 1856) has been accompanied by successive increases in size (wing length). Mathys and Lockwood (2009) showed that exotic great kiskadees (*Pitangus*

sulphuratus) on Bermuda had larger morphological dimensions than individuals from the source population on Trinidad 50 years after introduction. Mathys and Lockwood (2011) also showed that five out of six exotic passerine bird species they examined on the Hawaiian islands showed morphological divergence across islands 80 to 140 years after introduction, although they do not present comparisons with the source population. Amiot et al. (2007) demonstrated morphological divergence within an island by exotic red-whiskered bulbuls (*Pycnonotus jocosus*) over a period of around 30 years. Clines in body size have also been documented for exotic house sparrow and common myna (*Acridotheres tristis*) populations introduced to New Zealand in 1870, with a trend for larger body size in the northern parts of New Zealand (Baker and Moeed 1979, Baker 1980). Similar trends have also been observed in New Zealand exotic mammals (Yom-Tov et al. 1986), and in birds in other parts of the world (e.g. Johnston and Selander 1964, 1971, 1973). All of these patterns of divergence are indicative of changes in body size following establishment.

Here, we test for changes in body size between native and exotic populations for seven species of passerine bird introduced from the UK to New Zealand in the middle of the nineteenth century (Thomson 1922, McDowall 1994). We compare an aseasonal measure of body size - tarsus length - between specimens from present day New Zealand and present day UK, and between individuals from both these populations and individuals collected from the UK in the middle of the nineteenth century. Our expectation is that body sizes should be larger in New Zealand populations than in both historical and contemporary UK populations, based on the generally greater mean body size of island birds (Olson et al. 2009), evidence of size increases in natural avian colonists in New Zealand (Cassey and Blackburn 2004), and previous analyses of bird introductions (Mathys and Lockwood 2009) and invasions to islands (Clegg et al. 2002). As far as we are aware, this is the first time that the body sizes of individuals in exotic bird populations have been compared with individuals in historical source populations, rather than just with individuals in contemporary source populations that may also in theory have undergone morphological changes over the period since the exotic population was introduced.

Methods

We compared contemporary New Zealand (2003 – 2005; N = 140), contemporary UK (2005 – 2011; N = 175) and historical UK (1848 – 1879; N = 126) specimens of blackbird (*Turdus merula*), song thrush (*T. philomelos*), house sparrow (*Passer domesticus*), chaffinch (*Fringilla coelebs*), greenfinch (*Chloris chloris*), goldfinch (*Carduelis carduelis*) and yellowhammer (*Emberiza citrinella*). These species were chosen because specimens were available to us from all three populations of interest. Eight historical specimens of goldfinch (all from 1946), two of greenfinch (both from 1892) and one each of song thrush (1901 and house sparrow (1891) from New Zealand were also available for comparison, although the low sample sizes meant that we only formally

Table 1. Sample sizes of tarsus measurements included in the analysis for each population, together with the date of first known introduction into New Zealand from the UK.

	UK		New Zealand		
Species	**Historical**	**Contemporary**	**Historical**	**Contemporary**	**Date**
Blackbird	18	16		16	1862
Song thrush	8	14		15	1865
House sparrow	25	30		39	1862
Chaffinch	27	33		4	1862
Greenfinch	16	28		10	1862
Goldfinch	11	21	8	4	1862
Yellowhammer	21	6		23	1862

analysed these data for goldfinch. These goldfinch specimens date from midway between the date of introduction of this species to New Zealand and the contemporary New Zealand samples, but we may nevertheless predict some change between 1946 and the present. The historical UK specimens bracket the dates of first introduction to New Zealand of all these species (Table 1).

The contemporary New Zealand specimens sampled were all live birds caught opportunistically as part of fieldwork by John Ewen (J.E.) in New Zealand, spanning latitudes from Hauturu to Palmerston North (see Ewen et al. 2012 for a list of sites). The contemporary UK specimens were all frozen samples from the Garden Bird Health initiative (GBH*i*) archive. These specimens come from across England and Wales, although the majority (approximately two thirds) were from England south of the line connecting the Wash to the Severn Estuary. All were birds found dead by members of the public and submitted to the Institute of Zoology, where biometric measurements were recorded. Post mortem examinations were performed according to a standardised protocol and the carcasses with intact appendicular skeleton were archived at -20°C (Robinson et al., 2010). Carcasses with limb abnormalities or injury were excluded from the study. The specimens were partially defrosted and (with the exception of house sparrow) re-measured by J.E., under an extraction hood in the post-mortem room at the Institute of Zoology, using the same measurement method as for the contemporary New Zealand specimens. The historical specimens (UK and New Zealand) were all skins stored in the bird room of the Natural History Museum at Tring, UK. The majority of UK specimens were again from England south of the line connecting the Wash to the Severn Estuary (around 85%). The specimens were measured by J.E. using the same measurement method as for the contemporary samples.

We used tarsus length as our measure of body size. This is a measure of size that is invariant across seasons and is available for measurement on all the specimens available to us – most other standard aseasonal size measures, such as beak dimensions, wing chord and tail length, were not available on the post-mortemed GBH*i* specimens. Tarsus length was measured as full tarsus using dial Vernier callipers. Measurements were taken twice, with high repeatability: intraclass correlations (Bland and Altman 1996) varied from 0.94 for goldfinch (N = 108, 54 birds) to 0.985 for chaffinch (N

= 142, 71 birds). There is some evidence that drying specimens may cause changes to the dimensions of the skins, most often through shrinkage (e.g. Bjordal 1983, Winker 1993, Kuczynski et al. 2002), although dried tarsi may also be longer than when fresh (e.g. Herremans 1985), or show no significant change (e.g. Greenwood 1979). Bjordal's (1983) study is the only one that pertains to a species in our study: he found that house sparrow tarsi shrank by 1.1 – 1.3% on drying. Either way, it should be borne in mind that the historical (museum) specimens measured could differ from contemporary specimens as a consequence of preservation.

All specimens were measured by J.E. except for the contemporary house sparrow specimens from the GBH*i*, for which we used measurements taken by either Becki Lawson (B.L.; N = 28) or Katie Colvile (K.C.; N = 5) during the post-mortem examination. We tested for differences in the measurements made by J.E., B.L. and K.C. using paired t-tests to compare tarsus lengths taken from 25 GBH*i* specimens from 9 different bird species.

For all species except the song thrush, we analysed only birds that had been aged as adult. Birds were classed as juveniles until the post-juvenile body moult was complete. First year birds beyond their post-juvenile moult and adult birds were not differentiated. The tarsus is in any case fully grown at fledging and does not change thereafter, so we do not expect mis-aging of specimens to affect the results. The relative paucity of certain adults in the song thrush samples meant that we combined data from birds of all ages, and tests across all populations confirmed that there was no difference in tarsus length between adults, first years or birds of unknown age (ANOVA: $F_{2,35} = 0.115$, $P = 0.89$). We also excluded birds of unknown sex for all species except song thrush and goldfinch, for which many specimens could not be unambiguously identified as male or female.

We analysed models of tarsus length that included sex (male/female, or male/female/unknown), population (contemporary New Zealand, contemporary UK, historical UK; and for goldfinch, historical New Zealand), and their interaction, as factors. All analyses were carried out using ANOVA in R v. 2.14.1 (R Development Core Team 2006), with post-hoc comparisons between population means using Tukey's Honestly Significant Difference test. Regressions of tarsus length versus time with sex and location as factors cannot be applied in this case because there is only a single historical population for comparison. Sample sizes for the different populations for each species are given in Table 1, along with the date of first known introduction into New Zealand from the UK as recorded by Thomson (1922). We calculated the rate of change in a population in Darwins as $\ln(T2) - \ln(T1)/\Delta t$, where T2 equals contemporary tarsus length, T1 equals historical tarsus length, and Δt equals the time difference between the two populations in millions of years.

Results

Means and variances of tarsus lengths for each population of each species are given in Table 2. Full models for tarsus length as a function of population, sex, and their

Table 2. Mean and variance (mm) of tarsus length for each population of each species. % quantifies the change in each contemporary population relative to the UK historical mean, and equals 100 x (contemporary mean/UK historical mean). No measurements are available for historical New Zealand populations of blackbird, chaffinch and yellowhammer, and only single measurements for song thrush and house sparrow. Sample sizes are as in Table 1. The largest population mean for each species is given in bold, and the smallest in italics.

	UK			New Zealand		
Species	**Historical**	**Contemporary**	**%**	**Historical**	**Contemporary**	**%**
Blackbird	**39.43 ± 1.66**	*38.27 ± 0.87*	97.1		38.40 ± 0.99	97.3
Song thrush	**37.22 ± 1.97**	37.10 ± 0.85	99.6		*36.25 ± 1.33*	97.3
House sparrow	22.34 ± 1.39	*21.72 ± 0.96*	97.2		**23.07 ± 0.26**	103.3
Chaffinch	**21.93 ± 0.71**	*20.73 ± 0.42*	94.5		21.51 ± 0.55	98.1
Greenfinch	**21.72 ± 1.11**	*21.02 ± 0.40*	96.8		21.33 ± 0.33	98.2
Goldfinch	17.72 ± 0.92	*17.12 ± 0.22*	96.6	**17.81 ± 3.14**	17.56 ± 0.25	99.1
Yellowhammer	22.80 ± 0.40	*21.93 ± 0.64*	96.2		**22.92 ± 0.68**	100.5

Table 3. Results of ANOVA with tarsus length (mm) as the response variable and population, sex and their interaction, as predictor variables. d.f. = degrees of freedom for the comparison.

	Population		Sex		Interaction	
	F	**d.f.**	**F**	**d.f.**	**F**	**d.f.**
Blackbird	7.82***	2,59	1.24	1,59	0.69	2,59
Song thrush	1.67	2,30	1.73	2,30	0.31	2,30
House sparrow	20.05***	2,88	0.03	1,88	1.59	2,88
Chaffinch	17.12***	2,58	11.21***	1,58	0.50	2,58
Greenfinch	4.04*	2,48	0.83	1,48	0.98	2,48
Goldfinch	1.19	3,32	1.90	2,32	0.42	6,32
Yellowhammer	4.46*	2,44	0.83	1,44	3.25*	2,44

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

interaction, are given in Table 3 for all species. Sex was a significant predictor of tarsus length only for chaffinch, while the interaction between sex and location was significant only for yellowhammer. Population was a significant predictor of tarsus length for all species except song thrush and goldfinch. Figure 1 shows the median and variation in tarsus length across the various populations for each species, with sexes plotted separately for chaffinch and yellowhammer.

Contemporary UK populations have the shortest mean tarsus length for every species except the song thrush, for which the contemporary New Zealand populations are the smallest (Table 2). Birds from historical UK populations have the longest tarsus lengths for blackbird, song thrush, greenfinch, and chaffinch. Birds from contemporary New Zealand populations have the longest tarsus lengths for house sparrow and yellowhammer, while the longest goldfinch tarsi, on average, are possessed by historical New Zealand birds (Table 2). Contemporary means vary between 94.5% (UK chaffinch) and 103.3% (New Zealand house sparrow) of the UK historical means

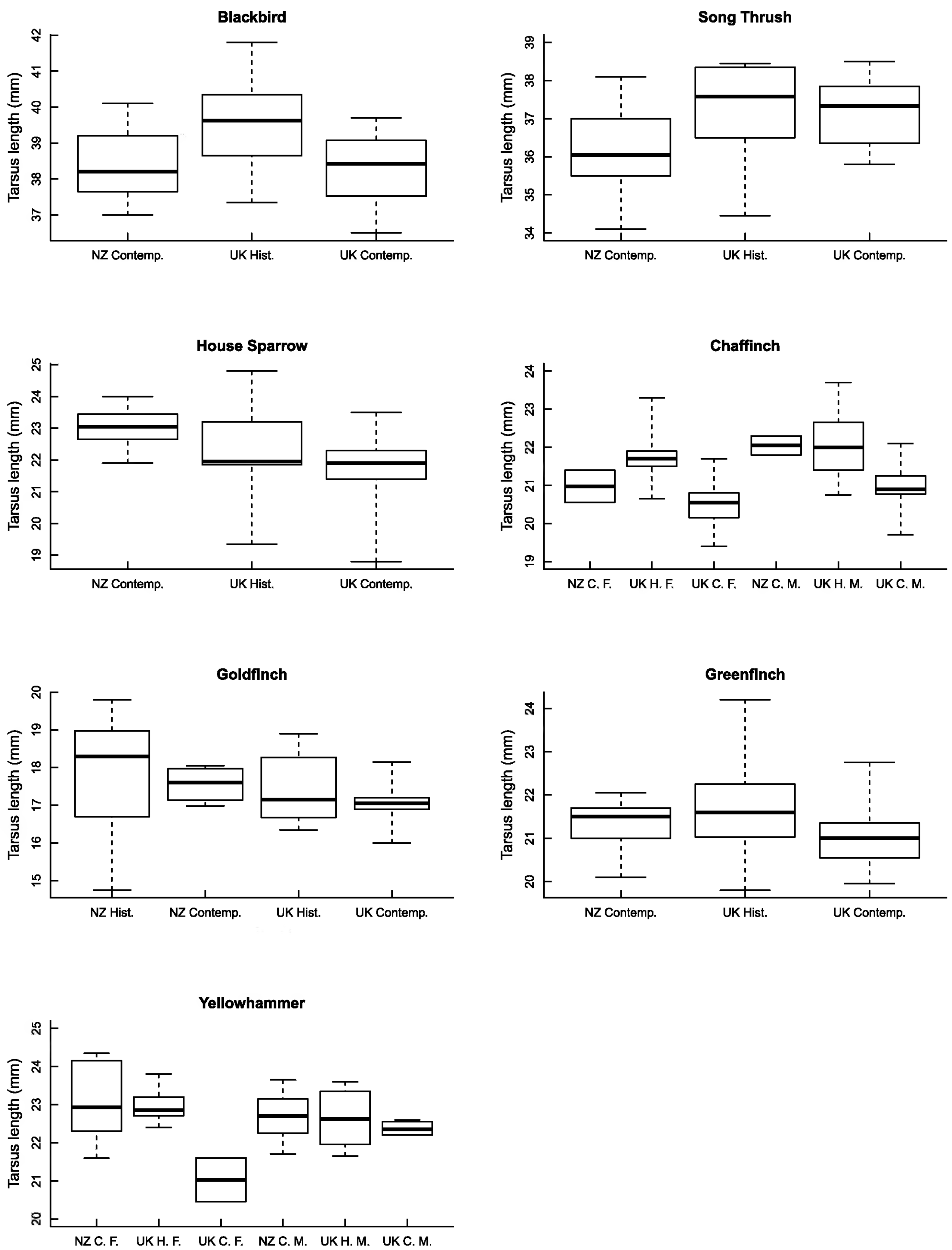

Figure 1. Box plots showing the median (dark line), quartiles (box), and range (whiskers) in tarsus length across the various populations for each species. Sexes are plotted separately for chaffinch and yellowhammer, as the models in Table 3 suggest sex differences for these species. NZ = New Zealand; Contemp. and C = contemporary; Hist. and H = historical; F = female; M = male.

for the species (Table 2). The average change in tarsus length between historical and contemporary means is 2.56%. The maximum absolute change in mean tarsus length is 1.2mm for the UK population of the chaffinch. This equates to a change of around 0.009 mm yr^{-1} given that the mean sample year was 1871 for historical specimens and 2006 for contemporary specimens, or –416 Darwins.

Post-hoc comparisons on the models plotted in Figure 1 reveal no significant differences between any of the populations for song thrush or goldfinch. For blackbird, birds from the historical UK population have longer tarsi than both contemporary UK (difference ± 95% confidence interval = 1.16 ± 0.91 mm, P = 0.009) and contemporary New Zealand (difference = 1.03 ± 0.91 mm, P = 0.023) birds. For house sparrow, birds from the contemporary New Zealand population have longer tarsi than both contemporary UK (difference = 1.34 ± 0.51 mm, P < 0.001) and historical UK (difference = 0.73 ± 0.54 mm, P = 0.005) birds. For greenfinch, birds from the historical UK population have longer tarsi than contemporary UK birds (difference = 0.69 ± 0.59 mm, P = 0.018). The same is true for chaffinch for both male (difference = 1.09 ± 0.75 mm, P < 0.001) and female (difference = 1.18 ± 0.88 mm, P = 0.002) birds. For yellowhammers, contemporary UK females are smaller than females from other populations, but the small sample size for this group (N = 2 females) and their unusually small tarsus lengths relative to all other groups (Figure 1) suggest that these results should not be over-interpreted. Significant differences have relatively high statistical power (mean sample size for significant comparisons = 47.2, mean for non-significant comparisons = 30.6; $F_{1,12}$ = 5.37, P = 0.039), but significant results do also have larger size changes than non-significant results (mean absolute percentage change = 3.52% vs 2.02%; $F_{1,12}$ = 4.94, P = 0.046), suggesting that power is not the only driver of significance.

Comparison of measurements obtained by the three different measurers from common specimens showed no significant differences in the measurements obtained by J.E. and K.C. (t = -1.68, N = 25, P = 0.11). However, estimates obtained by B.L. tended to be larger than those obtained by both J.E. (t = 5.47, N = 25, P < 0.001) and K.C. (t = 4.68, N = 25, P < 0.001).

Discussion

Increasing numbers of studies are providing evidence for morphological differences between introduced exotic and native source populations of species, for taxa as diverse as plants (e.g. Siemann and Rogers 2008), crustaceans (Torchin et al. 2001), reptiles (Losos et al. 1997), birds (Mathys and Lockwood 2009) and mammals (Simberloff et al. 2000). However, with the exception of experimental manipulations (e.g. Losos et al. 1997), previous studies have tested for morphological differences between contemporary exotic and native populations, rather than between contemporary exotic populations and the historical populations from which introduced individuals were taken. Any observed differences could therefore theoretically have arisen as a result

of morphological changes in the exotic population, the native population, or both (c.f. Gordon 1986); without historical data, it would be impossible to say which. Our measures of a morphological feature, tarsus length, from contemporary and historical specimens of a range of species introduced from the UK to New Zealand indeed show that changes have occurred not only in the exotic range, but also in the native range. In fact, contrary to expectations, the most common differences we found were between contemporary and historical UK populations. In the absence of historical size data, we would have greatly underestimated the frequency and extent to which morphological change was occurring in these bird populations.

In the 150 years or so since the seven species in our analysis were introduced from the UK to New Zealand, population mean tarsus lengths have changed by between 0.4 and 5.5%, with an average absolute change of 2.56%. Absolute changes have been greater in the UK populations, averaging 3.14% versus 1.97% in the New Zealand populations. The direction of change has been negative in 12 of the 14 populations, including in all seven UK populations. Contemporary UK populations have the shortest tarsi, on average, for six of the seven species measured. Significant decreases in tarsus length have occurred in the UK populations of blackbird, chaffinch and greenfinch, and in the New Zealand blackbird population. Our a priori expectation was for size increases in the New Zealand populations relative to the historical UK populations, but the only change that fitted this expectation, and indeed the only significant increase in size relative to the historical UK population, was for the house sparrow. The rate of change for the largest difference in these data, for the UK population of the chaffinch, is equivalent to –416 Darwins. This is larger than 89% of the rates of morphological change estimated by Millien (2006) for island populations of mammals. We cannot tell from these data whether the difference is the result of genetic adaptation or phenotypic plasticity (see e.g. Merilä 2012), but either way, it represents a relatively rapid size change.

Previous studies that have tested for morphological differences only between contemporary exotic and native populations may also fail to identify instances where morphological changes have occurred over time, if parallel changes occur in both populations. An example is provided in our data by the blackbird. Here, the contemporary UK and New Zealand populations do not differ significantly in tarsus length, but both contemporary populations have significantly shorter tarsi than the historical source population from the UK. Comparison of the contemporary populations would lead to the erroneous conclusion that no morphological change had occurred in the exotic population after introduction. It follows that the absence of any morphological difference between contemporary exotic and native populations does not necessarily mean that no changes have occurred in these populations over the period since the exotic population was introduced. One should not forget that native populations can change too, particularly in response to current human-induced environmental change.

A range of previous studies on body size in island birds led us to predict that species might increase in size following introduction to New Zealand. Islands tend to be home to the largest members of bird genera (Meiri et al. 2011), recent colonists to

New Zealand have smaller body sizes than their endemic relatives (Cassey and Blackburn 2004), and at least one recent natural colonist is larger in New Zealand than in its source population (Clegg et al. 2002). However, we do not in general find support for this hypothesis in the species analysed in this study. Only two species show increases in mean tarsus length in New Zealand relative to the historical source population, and only for the house sparrow is this increase significant. In contrast, five of the New Zealand populations show reductions in tarsus length following introduction, although again only one of these is significant (the blackbird). We can think of five explanations for the lack of concordance between these findings and our theoretical expectations.

First, tarsus length may not be a suitable measure of body size change in these populations, either because it does not adequately measure body size, or because it is not the relevant aspect of size. In respect to the adequacy of tarsus as a measure of size, Freeman and Jackson (1990) caution against using single metrics to quantify body size in small birds, but conclude that mass or tarsus length are the best single metrics to use. Conversely, Gosler et al. (1998) conclude that tarsus length is a poor measure of size in passerine birds. However, their reason – that the tarsus is fully grown at fledging and does not change thereafter – is actually an advantage for our analysis, as it means that our results are unlikely to be age-related artefacts. Moreover, their results show that tarsus length is commonly correlated with body mass within species of passerine bird. In respect of selection for changes in tarsus length on islands, a recent study of seven native bird species by Wright and Steadman (2012) showed that tarsi tended to be longer on the small island of Tobago than on larger Trinidad, or on the South American mainland. They attributed this difference to the greater variety of perching and foraging opportunities available on islands with reduced interspecific competition. Nevertheless, size changes in our context may be better assessed in terms of body mass than other measures of size, if different sizes on islands versus mainlands are due to intraspecific competition or thermal ecology (e.g. Clegg and Owens 2002). Body mass comparisons are harder to make accurately than are comparisons of tarsus length, as mass varies with individual condition and with season. In any case, body mass estimates are not available for all of the specimens available in this study, and indeed for none of the historical specimens.

Second, the time available since introduction to New Zealand may have been inadequate for the species concerned to have produced the predicted size changes. This seems unlikely. On the one hand, more than 100 generations have been available for size changes to occur in these species, if selection pressure for larger size exists. This has been enough time to produce geographic clines in body size in several exotic species in New Zealand (e.g. Baker and Moeed 1979, Baker 1980, Yom-Tov et al. 1986; but see Baker 1992) and elsewhere (e.g. Johnston and Selander 1964, 1971, 1973, Amiot et al. 2007). On the other, most of the observed size changes observed in New Zealand are decreases. While most of these changes are not significant, they are nevertheless not consistent with directional selection for larger body size, regardless of the time available for those selection pressures to have acted.

Third, there may in fact be no differences in the novel New Zealand versus the native UK environments that would lead to larger size in the former. This might seem

unlikely, as there is evidence from native species that birds do attain larger size on New Zealand (Cassey and Blackburn 2004), while the archipelago is also home to some notable examples of avian gigantism (e.g. *Dinornis* spp., *Notornis* spp., *Strigops habroptilus*). However, the conditions that lead to large size in the native species may have been altered by environmental changes following human colonization. Hypothesised drivers of size increases in small species, such as passerine birds, on islands include ecological release from competitors and predators, intensified intraspecific competition, and immigrant selection (Lomolino 2005). The fact that humans have introduced many species of small passerine bird and several species of mammalian predator (including brush-tailed possum *Trichosurus vulpecula*, rats *Rattus* sp., cats *Felis cattus*, and stoats *Mustela erminea;* King 2005), to a system previously free of such species, and have altered the immigration process by conducting these introductions, may therefore have removed exactly the pressures that drove body size changes in the native avifauna. As a result, the environment inhabited by the exotic species in New Zealand may not differ fundamentally from their native environment. If so, this suggests that one way to discriminate between different hypotheses for size increases in small species could be by relating size changes in exotic species to other changes to island environments. For example, if size changes were driven by a lack of predators on islands, we would predict that size changes in exotic prey species should only occur on islands on which exotic predators remain absent.

Fourth, those features of the environment that drove size increases in the native New Zealand avifauna may still apply, but may be being offset by new conditions. An obvious candidate is climate change. Official UK Department of Energy and Climate Change figures show that annual average temperatures in central England have increased by around 0.8–0.9°C in the period since bird species were introduced to New Zealand (http://www.decc.gov.uk/en/content/cms/statistics/climate_stats/data/data.aspx), with a similar increase in New Zealand over the last 100 years (http://www.climatechange.govt.nz/science). There is substantial global geographic variation in avian body sizes related to temperature, with species living at high latitudes and in cooler climates (and on islands) being generally larger-bodied than their relatives living at lower latitudes or in warmer climates (Olson et al. 2009). If the relationship were causal, climate warming would be expected to result in concomitant declines in the body size of species occupying an area. In line with this expectation, Yom-Tov (2001) demonstrated that the body sizes (masses and tarsus lengths) of several species of passerine declined in Israel over the second half of the twentieth century, while minimum summer temperatures increased over the same time period. The tendency for small decreases in body size in the introduced species in New Zealand may therefore reflect a trade-off between insularity and climate. Climate change may also explain why all seven UK populations show decreases in body size over time. Of course, this does not explain why size decreases were not ubiquitous: house sparrows tended to increase in size in New Zealand, but were one of the species shown by Yom-Tov (2001) to have decreased in tarsus length in Israel.

Climate is not the only aspect of the environment to have changed over the last 150 years. Agricultural intensification in the UK has led to farm landscapes with fewer areas

of non-crop, and lower densities of weeds and insects (Benton et al. 2002). Populations of farmland birds have suffered declines, including several of the species in our analysis (Gregory et al. 2004), in at least some cases as a result of the impact of declines in food availability on winter survival (Siriwardena et al. 1999). Food availability may also impact upon the body sizes attained by the remaining individuals, and cause the reductions seen here too. This explanation seems unlikely to explain the generally lower tarsus lengths for populations in New Zealand, however. The species analysed here typically attain densities an order of magnitude higher in New Zealand farmland versus farmland in the UK (MacLeod et al. 2009), while some of the New Zealand samples come from island nature reserves, which are not farmed and where pesticides and herbicides are not used.

Finally, the possibility that the differences between populations can be dismissed as methodological biases also needs to be considered. The first point to note here is that the small sample sizes available for some populations mean that observed differences – or lack thereof – should not be over-interpreted. Small sample sizes give less power to detect significant differences if they exist. This suggests if anything that the conclusions we base on our results are likely to be conservative, and yet we still found significant changes in tarsus length in most species. Small sample sizes will only be problematic for our conclusions if they are also biased. However, measurements of tarsus lengths for British populations of these species in the literature show a significant difference between sexes only for chaffinch (Cramp 1988, Cramp and Perrins 1994a, 1994b), which was also the only sex difference recovered in our analyses (Table 3). This suggests that the measurements on which our analyses are based are sufficiently accurate and reliable to be of use.

We can also exclude the possibility that differences between populations arise from effects of different measurers. All specimens were measured by J.E., except for the contemporary house sparrow carcasses, which were mainly measured by B.L. Comparisons between measurers showed that B.L. tended to produce longer tarsus measurements than J.E., yet contemporary UK house sparrow tarsi were shorter, on average, than both the contemporary New Zealand and historical UK tarsi measured by J.E.. The effect of different measurers for house sparrow populations means that the observed difference between contemporary UK and New Zealand populations of this species are likely to be conservative, and suggest also that the reduction in size between historical and contemporary UK populations is likely to be greater than that recorded in Table 2.

Differences between populations could, however, be the result of the different types of specimens measured – live birds versus defrosted carcasses versus dried skins. Drying of specimens can in some cases change tarsus length measurements, albeit that drying does not change tarsus lengths of all species in the same direction (c.f. Greenwood 1979, Bjordal 1983, Herremans 1985). Nevertheless, shrinkage seems to be more prevalent and more likely, and drying has been shown slightly to shrink tarsi for one species in our analysis, the house sparrow. However, dried specimens returned the largest population mean tarsus measurements for five of the seven species, while dried tarsi were larger than defrosted specimens in all seven species measured (Table 2). Freezing can also cause shrinkage in specimens if not done correctly, as freeze-drying can occur. While most of the smallest population mean tarsus lengths relate

to measurements made on defrosted carcasses, we think it unlikely that this is an effect of freeze-drying. All carcasses were stored at –20°C in knotted plastic bags inside sealed ziplock plastic bags, and were clearly moist on defrosting. Overall, the relatively large population mean tarsus measurements obtained from dried specimens, and the relatively small population means from frozen specimens, both seem unlikely to be consequences of these methods of preservation. A further possibility is that the frozen individuals were dead carcasses found by members of the public, and may not be representative samples of the populations concerned if smaller individuals are more likely to be found dead. In fact, any or all of the samples we analyse could be biased in unknown ways by collection methods, but in the absence of any evidence on this score, we assume that the samples are unbiased estimates of population parameters.

Differences between populations could also be a consequence of differences in where individuals were sampled, as there is geographic variation in body size across geographic ranges within bird species (Ashton 2002), including in at least two of the species in our samples (Murphy 1985, Merilä 1997). This is unlikely to drive the differences we observed between contemporary and historical UK populations, however, as the majority of specimens in both samples were from the southern half of the UK, and therefore sample only a small proportion of the total native range of the species analysed. The New Zealand samples are also relatively limited in spatial extent; all derive from the northern half the country (Ewen et al. 2012), from sites spanning around 4° of latitude. These exotic populations derived from releases of birds from the UK (thought most likely to have been captured near the major ports in southern England) undertaken by acclimatisation societies in Auckland and Wellington (Thomson 1922), and size differences must then have developed *in situ*. We cannot see how sample site choice in New Zealand could bias comparisons with UK populations. A bias could occur if birds of a certain size were more likely to survive the journey (e.g. smaller blackbirds and larger house sparrows), but we can provide no evidence either way on this point.

In conclusion, comparison of tarsus lengths in contemporary native UK and exotic New Zealand populations of seven passerine bird species reveals a significant difference in only one species, the house sparrow. However, consideration of contemporary populations alone masks the fact that significant changes in tarsus length have occurred over the last 150 years in five populations of four species, and therefore underestimates the true scale of morphological change in these populations over time. UK populations of blackbird, chaffinch and greenfinch, and the New Zealand population of the blackbird have all significantly decreased in size, while house sparrows in New Zealand have significantly increased. Why these particular populations should show significant changes in size over the last 150 years, while others show no changes, is unclear. There are no obvious features of location, species, life history, or gross ecology that relate to this variation. Thus, it remains of considerable interest to explain why some populations have changed in morphological size (tarsus length), but not others (assuming that there is more than simply idiosyncratic or stochastic change occurring), and in addition, whether these changes are the result of phenotypic plasticity or genetic adaptation.

Acknowledgements

We thank Mark Lomolino, Shai Meiri, Virginie Millien and Ally Phillimore for comments that greatly improved an earlier version of this manuscript, Shinto John for helping with access to the GBH*i* carcasses, Katie Colvile for assistance with measuring contemporary house sparrow specimens, Robert Prys-Jones and other staff at the Natural History Museum, Tring, for access to historical specimens, and the King Saud University Distinguished Scientist Fellowship Programme for funding assistance. The GBH*i* received financial support from the Universities Federation for Animal Welfare, the RSPB, Defra, CJ Wildbird Foods, Gardman Ltd., Cranswick Pet Products, Tom Chambers Ltd., the Birdcare Standards Association and the BVA Animal Welfare Foundation. We thank the members of the public and participants in the British Trust for Ornithology's Garden BirdWatch who submitted carcasses to the GBH*i* for post mortem examination. P.C. is an ARC Future Fellow (FT0991420).

References

Amiot C, Lorvelec O, Mandon-Dalger I, Sardella A, Lequilliec P, Clergeau P (2007) Rapid morphological divergence of introduced Red-whiskered Bulbuls *Pycnonotus jocosus* in contrasting environments. Ibis 149: 482–489. doi: 10.1111/j.1474-919X.2007.00671.x

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. Ibis 103b: 458–473. doi: 10.1111/j.1474-919X.1963.tb06766.x

Ashton KG (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecology and Biogeography 11: 505–523. doi: 10.1046/j.1466-822X.2002.00313.x

Baker AJ (1980) Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). Evolution 34: 638–653. doi: 10.2307/2408018

Baker AJ, Moeed A (1979) Evolution in the introduced New Zealand population of the common myna. Canadian Journal of Zoology 57: 570–584. doi: 10.1139/z79-067

Benton TG, Bryant DM, Cole L, Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology 39: 673–687. doi: 10.1046/j.1365-2664.2002.00745.x

Bjordal H (1983) Effects of deep freezing, freeze-drying and skinning on body dimensions of house sparrows (*Passer domesticus*). Cinclus 6: 105–108.

Blackburn TM, Lockwood JL, Cassey P (2009) Avian Invasions. The ecology and evolution of exotic birds. Oxford University Press, Oxford.

Bland JM, Altman DG (1996) Measurement error and correlation coefficients. British Medical Journal 313: 41–42. doi: 10.1136/bmj.313.7048.41

Briskie JV, Mackintosh M (2004) Hatching failure increases with severity of population bottlenecks in birds. Proceedings of the National Academy of Sciences, USA 101: 558–561. doi: 10.1073/pnas.0305103101

Cassey P, Blackburn TM (2004) Testing a macro-evolutionary relationship using a Holocene island bird assemblage. Ecography 27: 59–67. doi: 10.1111/j.0906-7590.2004.03585.x

Cassey, P Blackburn TM, Evans KL (2005) Correlated changes in reproductive effort of exotic passerines. Notornis 52: 243–246.

Clegg SM, Degnan SM, Kikkawa J, Moritz C, Estoup A, Owens IPF (2002) Genetic consequences of sequential founder events by an island-colonizing bird. Proceedings of the National Academy of Sciences, USA 99: 8127–8132. doi: 10.1073/pnas.102583399

Clegg SM, Owens IPF (2002) The 'island rule' in birds: medium body size and its ecological explanation. Proceedings of the Royal Society B 269: 1359–1365. doi: 10.1098/rspb.2002.2024

Covas R (2011) Evolution of reproductive life histories in island birds worldwide. Proceedings of the Royal Society B, 279, 1531–1537. doi: 10.1098/rspb.2011.1785

Cramp S (1988) (Ed) Birds of the Western Palaearctic. Volume V. Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Cramp S, Perrins CM (1994a) (Eds) Birds of the Western Palaearctic. Volume VIII. Crows to finches. Oxford University Press, Oxford.

Cramp S, Perrins CM (1994b) (Eds) Birds of the Western Palaearctic. Volume IX. Buntings and New World warblers. Oxford University Press, Oxford.

Davis MA (2009) Invasion Biology. Oxford University Press, Oxford

Duncan RP, Blackburn TM, Cassey P (2006) Factors affecting the release, establishment and spread of introduced birds in New Zealand. In: RB Allen, Lee WG (Eds) Biological invasions in New Zealand, Springer, 137–154. doi: 10.1007/3-540-30023-6_9

Evans KL, Duncan RP, Blackburn TM, Crick HQP (2005) Geographical variation in avian clutch size: testing Ashmole's hypothesis using introductions as a natural experiment. Functional Ecology 19: 616–624. doi: 10.1111/j.1365-2435.2005.01016.x

Ewen JG, Bensch S, Blackburn TM, Bonneaud C, Brown R, Cassey P, Clarke R, Perez-Tris J (2012) Exotic parasite establishment: The origins and characteristics of an avian malaria community in an isolated island avifauna. Ecology Letters 15: 1112–1119. doi: 10.1111/j.1461-0248.2012.01833.x

Freeman S, Jackson WM (1990) Univariate metrics are not adequate to measure avian body size. Auk, 107, 69–74.

Futuyma DJ (1979) Evolutionary Biology. 1st edition. Sinauer Associates, Sunderland, Massachusetts.

Gordon KR (1986) Insular evolutionary body size trends in *Ursus*. Journal of Mammalogy 67: 395–399. doi: 10.2307/1380895

Gosler AG, Greenwood JJD, Baker JK, Davidson NC (1998) The field determination of body size and condition in passerines: a report to the British Ringing Committee. Bird Study 45: 92–103. doi: 10.1080/00063659809461082

Greenwood JG (1979) Post-mortem shrinkage of Dunlin *Calidris alpina* skins. Bulletin of the British Ornithological Club 99: 143–145.

Gregory RD, Noble DG, Custance J (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. Ibis 146 s2: 1–13. doi: 10.1111/j.1474-919X.2004.00358.x

Haldane JBS (1949) Suggestions as to quantitative measurement of rates of evolution. Evolution 3: 51–56. doi: 10.2307/2405451

Herremans M (1985) Post-mortem changes in morphology and its relevance to biometrical studies. Bulletin of the British Ornithological Club 105: 89–91.

IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri RK, Reisinger A (Eds)] IPCC, Geneva, Switzerland, 104 pp.

Johnston RF, Selander RK (1964) House sparrows: rapid evolution of races in North America. Science 144: 548–550. doi: 10.1126/science.144.3618.548

Johnston RF, Selander RK (1971) Evolution in the house sparrow. II. Adaptive differentiation in North American populations. Evolution 25: 1–28. doi: 10.2307/2406496

Johnston RF, Selander RK (1973) Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. American Naturalist 107: 373–390. doi: 10.1086/282841

King CM (2005) The handbook of New Zealand mammals. Oxford University Press, Oxford.

Kuczynski L, Tryjanowski P, Antczak M, Skoracki M, Hromada M (2002) Repeatability of measurements and shrinkage after skinning: the case of the Great Grey Shrike *Lanius excubitor*. Bonner zoologische Beiträge 51: 127–130.

Lomolino MV (2005) Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32: 1683–1699. doi: 10.1111/j.1365-2699.2005.01314.x

Long JL (1981) Introduced birds of the world. The worldwide history, distribution and influence of birds introduced to new environments. David & Charles, London.

Losos JB, Warheitt KI, Schoener TW (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387: 70–73. doi: 10.1038/387070a0

MacLeod CJ, Newson SE, Blackwell G, Duncan RP (2009) Enhanced niche opportunities: can they explain the success of New Zealand's introduced bird species? Diversity and Distributions, 15, 41–49. doi: 10.1111/j.1472-4642.2008.00498.x

McDowall RM (1994) Gamekeepers for the nation: the story of New Zealand's acclimatisation societies 1861–1990. Canterbury University Press, Christchurch, New Zealand.

Mathys BA, Lockwood JL (2009) Rapid evolution of great kiskadees on Bermuda: an assessment of the ability of the island rule to predict the direction of contemporary evolution in exotic vertebrates. Journal of Biogeography 36: 2204–2211. doi: 10.1111/j.1365-2699.2009.02169.x

Mathys BA, Lockwood JL (2011) Contemporary morphological diversification of passerine birds introduced to the Hawaiian archipelago. Proceedings of the Royal Society B 278: 2392–2400. doi: 10.1098/rspb.2010.2302

Meiri S, Raia P, Phillimore AB (2011) Slaying dragons: limited evidence for unusual body size evolution on islands. Journal of Biogeography 38: 89–100. doi: 10.1111/j.1365-2699.2010.02390.x

Merilä J (1997) Quantitative trait and allozyme divergence in the greenfinch (*Carduelis chloris*, Aves: Fringillidae). Biological Journal of the Linnean Society 61, 243–266.

Merilä J (2012) Evolution in response to climate change: In pursuit of the missing evidence. BioEssays 34: 811–818. doi: 10.1002/bies.201200054

Millien V (2006) Morphological evolution is accelerated among island mammals. PLoS Biology 4: e321. doi: 10.1371/journal.pbio.0040321

Murphy EC (1985) Bergmann's rule, seasonality, and geographic variation in body size of house sparrows. Evolution 39: 1327–1334. doi: 10.2307/2408789

Olson V, Davies RG, Orme CDL, Thomas GH, Meiri S, Blackburn TM, Gaston KJ, Owens IPF, Bennett PM (2009) Global biogeography and ecology of body size in birds. Ecology Letters 12: 249–259. doi: 10.1111/j.1461-0248.2009.01281.x

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge. doi: 10.1017/CBO9780511608551

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robertson CJR, Hyvonen P, Fraser MJ, Pickard CR (2007) Atlas of bird distribution in New Zealand 1999–2004. The Ornithological Society of New Zealand Inc., Wellington.

Robinson RA, Lawson B, Toms MP, Peck KM, Kirkwood JK (2010) Emerging infectious disease leads to rapid population declines of common British birds. PLoS ONE 5(8): e12215. doi: 10.1371/journal.pone.0012215

Samaš P, Grim T, Hauber ME, Cassey P, Weidinger K, Evans KL (2013) Ecological predictors of reduced avian reproductive investment in the southern hemisphere. Ecography 36: in press.

Siemann E, Rogers WE (2008) Genetic differences in growth of an invasive tree species. Ecology Letters 4: 514–518. doi: 10.1046/j.1461-0248.2001.00274.x

Simberloff D, Dayan T, Jones C, Ogura G (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81: 2086–2099.

Siriwardena GM, Baillie SR, Wilson JD (1999) Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. Ibis 141: 621–636. doi: 10.1111/j.1474-919X.1999.tb07370.x

Thomson GM (1922) The naturalisation of plants and animals in New Zealand. Cambridge University Press, Cambridge. doi: 10.5962/bhl.title.28093

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions 3: 333–345. doi: 10.1023/A:1015855019360

Winker K (1993) Specimen shrinkage in Tennessee warblers and 'Traill's' flycatchers. Journal of Field Ornithology 64: 331–336.

Wright NA, Steadman DW (2012) Insular avian adaptations on two Neotropical continental islands. Journal of Biogeography 39: 1891–1899. doi: 10.1111/j.1365-2699.2012.02754.x

Yom-Tov Y (2001) Global warming and body mass decline in Israeli passerine birds. Proceedings of the Royal Society B 268: 947–952. doi: 10.1098/rspb.2001.1592

Yom-Tov Y, Green WO, Coleman JD (1986) Morphological trends in the common brushtail possum, *Trichosurus vulpecula*, in New Zealand. Journal of Zoology 208: 583–593.

Yom-Tov Y, Yom-Tov S, Moller H (1999) Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. Journal of Biogeography 26: 947–958. doi: 10.1046/j.1365-2699.1999.00338.x